




First record of the Gangetic Swamp Eel, *Ophichthys cuchia* (Hamilton, 1822) (Teleostei: Synbranchidae), from Texas (USA) based on museum vouchered material, and confirmation of a second established non-native population in the USA

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Abstract

The native range of *Ophichthys cuchia* includes part of Bangladesh, Bhutan, India, Myanmar, and Nepal. *Ophichthys cuchia* has also been collected within six states in the USA (Louisiana, Maryland, Michigan, New Jersey, New York, and Pennsylvania) and an established invasive population exists in New Orleans (Louisiana). We provide the first record of *O. cuchia* from Texas and the second report of an established non-native population in the USA based on 26 museum vouchered specimens collected from a series of urban ponds within the Houston metro area (Fort Bend Co.).

Keywords

Houston metro area, invasive species, North America

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Introduction

The swamp eel genus *Ophichthys* Swainson, 1839 includes synbranchid eels (Synbranchiformes, Synbranchidae), previously placed in the catch-all genus “*Monopterus*”, that exhibit scales on the body, a pair of suprabranchial pouches, and a reduced gill-arch skeleton in which several elements are missing (Britz et al. 2020). Following Britz et al. (2020), *Ophichthys* contains five species, including *O. cuchia* (Hamilton, 1822), *O. fossorius* (Nair, 1952), *O. indicus* (Silas & Dawson, 1961), *O.*

desilvai (Bailey & Gans, 1998), and *O. ichthyophoides* (Britz, Lalremsanga, Lalrotluanga & Lalramliana, 2011), and likely also *O. hodgarti* (Chaudhuri, 1913) (Britz et al. 2020, 2021).

With the exception of *O. cuchia*, the species of *Ophichthys* exhibit narrow ranges in northern India (*O. ichthyophoides*, *O. hodgarti*), southern India (*O. indicus*, *O. fossorius*), and Sri Lanka (*O. desilvai*) and are known from relatively few specimens (Bailey and Gans

1998; Britz et al. 2011, 2020a, 2020b, 2021). *Ophichthys cuchia* is widespread and distributed throughout much of northern India, and the adjacent countries of Bangladesh, Bhutan, Myanmar, and Nepal (Talwar and Jhingran 1991; Nico et al. 2019). This species is relatively well studied and, unlike other synbranchids, does not exhibit protogynous hermaphroditism (Liem 1968). It has become an important food fish in South Asia, especially in Bangladesh where it is collected year-round and exported live to markets throughout Asia, Australasia, and North America (Nico et al. 2019).

The international trade of *O. cuchia* and other synbranchids [e.g., *Monopterus albus* (Zuiew, 1793) and *M. javanensis* Lacépède, 1800] has resulted in the introduction of these fishes to areas outside of the native range, including water bodies throughout Asia, Australia, Canada, and the USA (Nico et al. 2019). In many cases, the introduction of *O. cuchia* to areas outside of the native range has been linked to prayer-release rituals, including in USA, where this species has been collected from water bodies in Louisiana, Maryland, Michigan, New Jersey, New York, and Pennsylvania (Fig. 1A; Nico et al. 2019; Jordan et al. 2020). Perhaps due to extreme winter temperatures, *O. cuchia* has not yet become established in the more northern of these six states (Nico et al. 2019),

but an established non-native population of *O. cuchia* was recently reported from the southern state of Louisiana (Jordan et al. 2020). This non-native population is currently restricted to a short stretch of Bayou St. John, a highly modified urban system in the New Orleans metro area, which is connected to Lake Pontchartrain. In their study, Jordan et al. (2020) briefly noted a potentially established, non-native population of *O. cuchia* in the Houston metro area, Texas (A. Best pers. comm. to F. Jordan). In this paper, we expand on the earlier report of *O. cuchia* from Texas based on the collection of multiple individuals, over multiple collection events, from a series of small retention ponds in Buffalo Run Park in the Houston metro area, Fort Bend Co., Texas (Fig. 1B, C). Based on the number of collection events, the number of specimens collected, and the size range exhibited (TL 154.0–768.0 mm), we conclude that this species has become established in Texas at this locality.

Methods

We followed Britz et al. (2020) and use the generic name *Ophichthys* for *O. cuchia* and congeners because it has priority over *Amphipnous* Müller, 1840. We sampled for freshwater fishes at Buffalo Run Park (Fort Bend Co.,

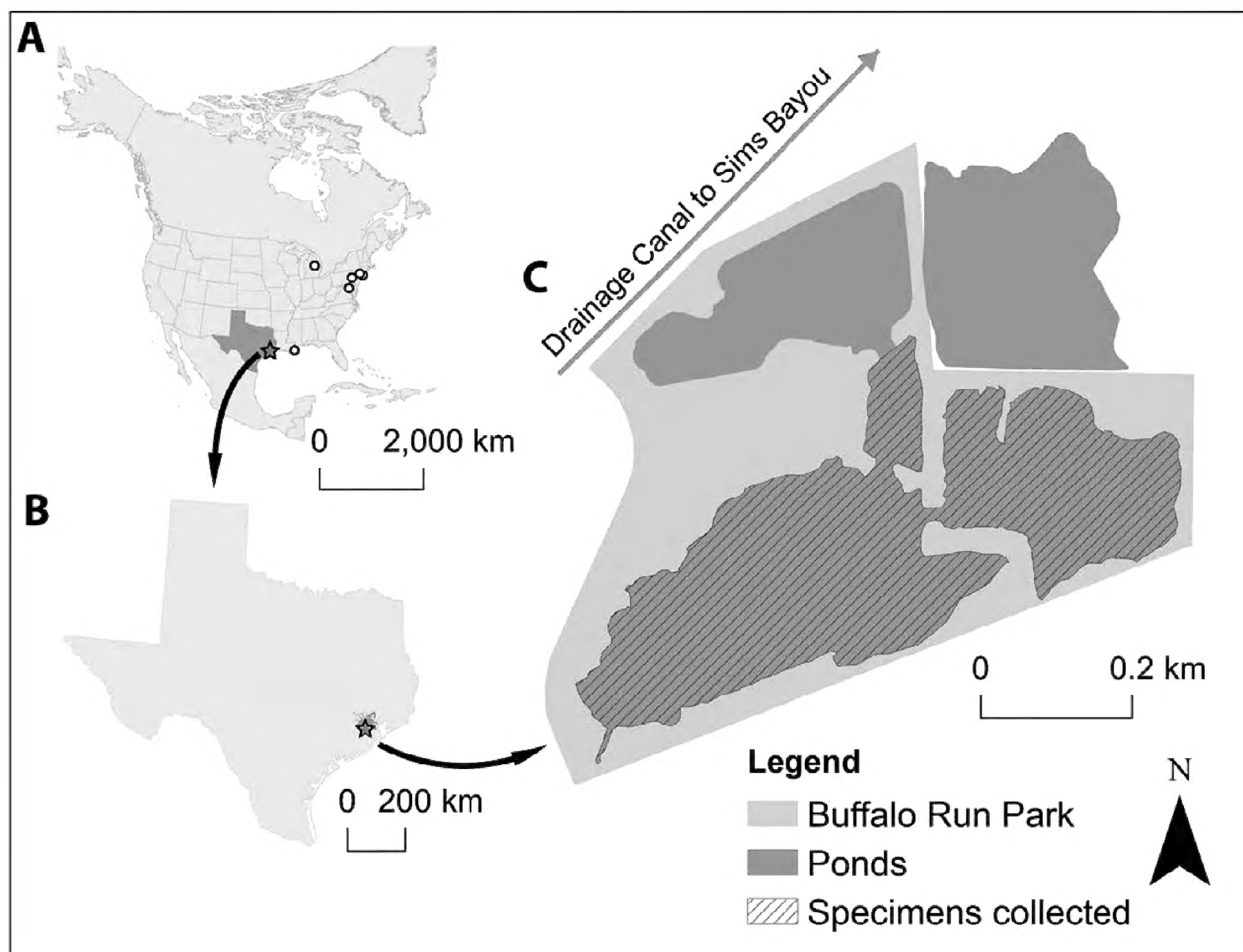


Figure 1. New record of the non-native *Ophichthys cuchia* in Texas, USA. **A.** Geographic distribution of the species in USA based on literature records (white circles), new Texas record represented by yellow star, state of Texas shaded grey. **B.** Location of the greater Houston area within Texas (dark grey), location of Buffalo Run Park represented by yellow star. **C.** Five ponds within or near to Buffalo Run Park in Fort Bend Co., Texas, from which specimens of *O. cuchia* were collected (diagonal stripes).

TX, USA; Fig. 1C) on four separate occasions (30 July 2019, 5 March 2020, 10 March 2021, and 20 October 2021). Specimens were collected using electricity delivered from two aluminum boats; one equipped with a Midwest Lakes Electrofishing Systems Infinity HC-80 unit and the other from a Smith-Root 7.5 Generator Powered Pulsator (GPP) unit. Stunned fish were collected using either a dip net or trident attached to the end of 3-m long fiberglass poles. Once collected, fish were euthanized using an ice slurry and stored on ice until returned to the laboratory, where they were fixed in a 10% solution of buffered formalin for 1 week before being transferred to 70% ethanol for final storage. Prior to fixation in formalin, a tissue sample (small plug of muscle) was removed from the right side of select specimens and stored in 95% ethanol. Specimens and associated tissues were deposited at the Biodiversity Research and Teaching Collections, Texas A&M University, College Station, TX, USA (TCWC).

Total length (TL) was measured from the tip of the snout to the posterior tip of the body (potentially damaged and regrown in some specimens). Two specimens (TCWC 20167.01, TL 393.7 mm and 469.9 mm) were radiographed at the Texas A&M University Veterinary Medical Teaching Hospital. A pin was inserted into the anus to mark the location of this structure during radiography following Bailey and Gans (1998). Counts of pre-anal vertebrae (all vertebrae anterior to the anus; Bailey and Gans, 1998) and abdominal vertebrae (all vertebrae anterior to the first vertebrae to bear a hemal spine) were obtained from radiographs. The total number of vertebrae could not be counted from the radiographs that we obtained because the tiny posterior-most centra were not visible. We also removed the alimentary canal from five individuals to assess stomach contents.

Genomic DNA was extracted from tissue samples (small plug of muscle) obtained from four individuals of *O. cuchia* using a DNeasy Tissue Extraction Kit (Qiagen, Inc., Valencia, CA, USA) and following the manufacturer protocols. A segment of the mitochondrial cytochrome c oxidase subunit I gene (COI) was amplified using polymerase chain reaction (PCR) and the primer pair Fish F1/R1 (Ward et al. 2005). PCR conditions included an initial denaturation at 94 °C for 4 min, then 35 cycles at 94 °C for 30 s each, 54 °C for 30 s, and 72 °C for 1 min, followed by a final extension at 72 °C for 10 min and were performed in 25.0 µl volumes, containing 12.5 µl of GoTaq Green Master Mix (Promega, Madison, WI, USA), 10.95 µl of nuclease-free water, 300 ng of template DNA, and 10 µM each of forward and reverse primer. Amplified PCR product was sequenced using the high-throughput sequencing facilities at Psomagen, Inc (Rockville, MD, USA). Obtained sequences were checked for accuracy of base determination and assembled using SEQUENCHER v. 5.4.6 (Gene Codes Corporation, Ann Arbor, MI, USA). The final sequences have been deposited on Genbank (accession numbers listed in Appendix Table A1).

Sequences obtained in this study and 26 additional COI sequences representing the genus *Ophichthys* and *Monopterus* obtained from GenBank (see Appendix Table A1) were aligned by eye using BBEdit (Bare Bones Software Inc., Bedford, MA, USA). Genetic distances (uncorrected *p*-distances) between sequences were obtained using MEGA v. 10 (Kumar et al. 2018). To visualise relationships between haplotypes for three species of *Ophichthys* (*O. cuchia*, *O. indicus*, and *O. fossilis*), a median-joining network (Bandelt et al. 1999) was constructed in PopART (Leigh et al. 2015). A maximum-likelihood (ML) analysis of the aligned dataset of 30 COI sequences was conducted using GARLI v. 0.951 (Zwickl 2006). We conducted 100 bootstrap replicates and searched for the best scoring ML tree simultaneously in a single analysis with all parameters set to default. The resulting best scoring ML phylogram was rooted with *Monopterus albus* and viewed using FIG-TREE v. 1.4.4 (<http://tree.bio.ed.ac.uk/software/figtree>).

Results

Ophichthys cuchia (Hamilton, 1822)

New records. UNITED STATES OF AMERICA – Texas • Fort Bend Co., Missouri City, Buffalo Run Park; 29°36'52.0"N, 095°30'46.6"W; 0.1–0.5 m depth; 30.VI.2019; A. Best; GenBank: OL807622–25; 7 specimens, sex indet., 397.0–768.0 mm TL, TCWC 20167.01 • same locality; 5.III.2020; A. Best, R. Britz, K.W. Conway, K. Kubicek, A.K. Pinion; 1 specimen, sex indet., not measured, TCWC 20288.01 • same locality; 10.III.2021; A. Best, K.W. Conway, J.S. Perkin, L. Elkins, 5 specimens, sex indet., 420.0–672.0 mm TL, TCWC 20465.01 • same locality; 20.X.2021; W. Arend, A. Best, H. Binkley, J.S. Perkin, R. Mangold, J. Wolff, 13 specimens, sex indet., 154.0–736.6 mm TL, TCWC 20323.01.

Buffalo Run Park includes four hydrologically connected ponds constructed from flooded open-pit sand mines and lies adjacent to a fifth, private pond that was part of the original mine and is separated from the public water by a low elevation levee (Fig. 1C). Water level in the ponds is maintained through groundwater influence. The ponds range in size from 1.05–10.45 ha and depth from 0.5–8.0 m. *Ophichthys cuchia* was collected from shallow water (0.1–0.5 m) along the edge of three of the five ponds (Fig. 1C). The majority of this littoral habitat was littered with submerged branches, and leaf litter over a substrate of mud and sand, and shaded by overhanging bank vegetation, including grasses and tree branches. Sections of littoral habitat were composed of hard substrate items with interstitial cavities, such as rock, cement slabs, and metal refuse. Discarded items were abundant in all shallow water along the shoreline, including aluminum cans, plastic debris, and fabric. *Ophichthys cuchia* was collected from areas with both hard and soft substrates, and utilized cavities in both, the bank or mud substrate and cavities between rocks/

cement slabs as refuge. Other species encountered in the same habitat included members of Cyprinidae [*Pimephales vigilax* (Baird & Girard, 1853), *Cyprinus carpio* Linnaeus, 1758], Poeciliidae [*Gambusia affinis* (Baird & Girard, 1853)], Centrarchidae [*Lepomis macrochirus* Rafinesque, 1810, *L. megalotis* Rafinesque, 1820, *Micropterus salmoides* (Lacepède, 1802)], and Cichlidae (*Oreochromis* sp.). Other species encountered in deeper areas of the same ponds included members of Clupeidae [*Dorosoma cepedianum* (Lesueur, 1818)], Cyprinidae [*Cyprinus carpio*, *Carassius carassius* (Linnaeus, 1758), *Ctenopharyngodon idella* (Valenciennes in Cuvier & Valenciennes, 1844)], and Loricariidae (*Pterygoplichthys* sp.).

Only two of the five stomachs of *O. cuchia* examined (all from TCWC 20167.01) had content. The stomach of one specimen contained a single, partially digested *L. macrochirus* and another contained a single partially digested *M. salmoides*. The mesentery surrounding the gut of all five individuals dissected contained large numbers of unidentified nematodes.

Identification. Following the original description by Hamilton (1822; original color plate accompanying description published as plate IV in Britz 2019) and the account in Talwar and Jhingran (1991), *O. cuchia* can be identified by the following combination of characters (Figs. 2, 3): anterior nostril located close to tip of snout and posterior to upper lip; posterior nostril above eye; eye located on upper and anterior part of head, close to snout; gill opening U-shaped, restricted to ventral midline; scales absent from head; scales on body tiny, cycloid, present over entire body surface (Fig. 3D, E); all median and paired fins absent; posterior part of body with low dorsal- and anal-fin folds; posterior tip of body, when intact, terminates in a narrow point. Aspects of live color pattern are also useful for identification including: presence of numerous small, dark brown, circular to oval spots over entire body; an olive-brown background

color on the body; and presence of multiple paired pale to bright yellow, roughly horizontal lines of varying length over head and body, including a longer pair on anterodorsal part of body, shifting to center of body around midpoint, and numerous shorter pairs on the posterodorsal and posterolateral part of head posterior to eyes (Fig. 3). Numerous short, pale to bright yellow, vertical lines of varying length are also present over the body surface (Fig. 3). We suspect that the pale to bright yellow lines mark the location of the lateral line system (pit lines) on the surface of the body (not investigated further). Vertebral counts for two specimens are 93 and 95 pre-anal, and 99 and 102 abdominal vertebrae, respectively. The counts of 99 and 102 abdominal vertebrae fall within the range of abdominal vertebrae reported for *O. cuchia* by Rosen and Greenwood (1976).

Intraspecific differences (uncorrected *p*-distances) between the 27 COI sequences of *O. cuchia* investigated were low and ranged from 0–1.9%, suggesting that the individuals from Bangladesh, India, and Texas from which the sequences were obtained are likely conspecific. For comparison, interspecific differences between COI sequences of the three species of *Ophichthys* (*O. cuchia*, *O. fossorius*, and *O. indicus*) ranged from 11.8–12.8%. The 27 COI sequences of *O. cuchia* represented nine mitochondrial haplotypes, including four unique and five shared haplotypes. The four individuals from Fort Bend Co., Texas, represented three haplotypes, including one unique haplotype and two of the shared haplotypes (Fig. 4A). The two most common haplotypes were shared by individuals from Bangladesh, India, and Texas (Fig. 4A). The ML phylogram resulting from the analysis of the COI dataset includes three lineages within a monophyletic *Ophichthys*: *O. cuchia* (represented by 27 sequences), *O. fossorius* (1 sequence), and *O. indicus* (1 sequence). Branch lengths within the *O. cuchia* lineage in the ML phylogram are extremely short (Fig. 4B) and there is limited geographic clustering within the larger



Figure 2. *Ophichthys cuchia*, TCWC 20167.01. **A.** 393.7 mm TL. **B.** Radiograph of the same individual shown in A. **C.** 470.0 mm TL, radiograph. A–C represent composite images.

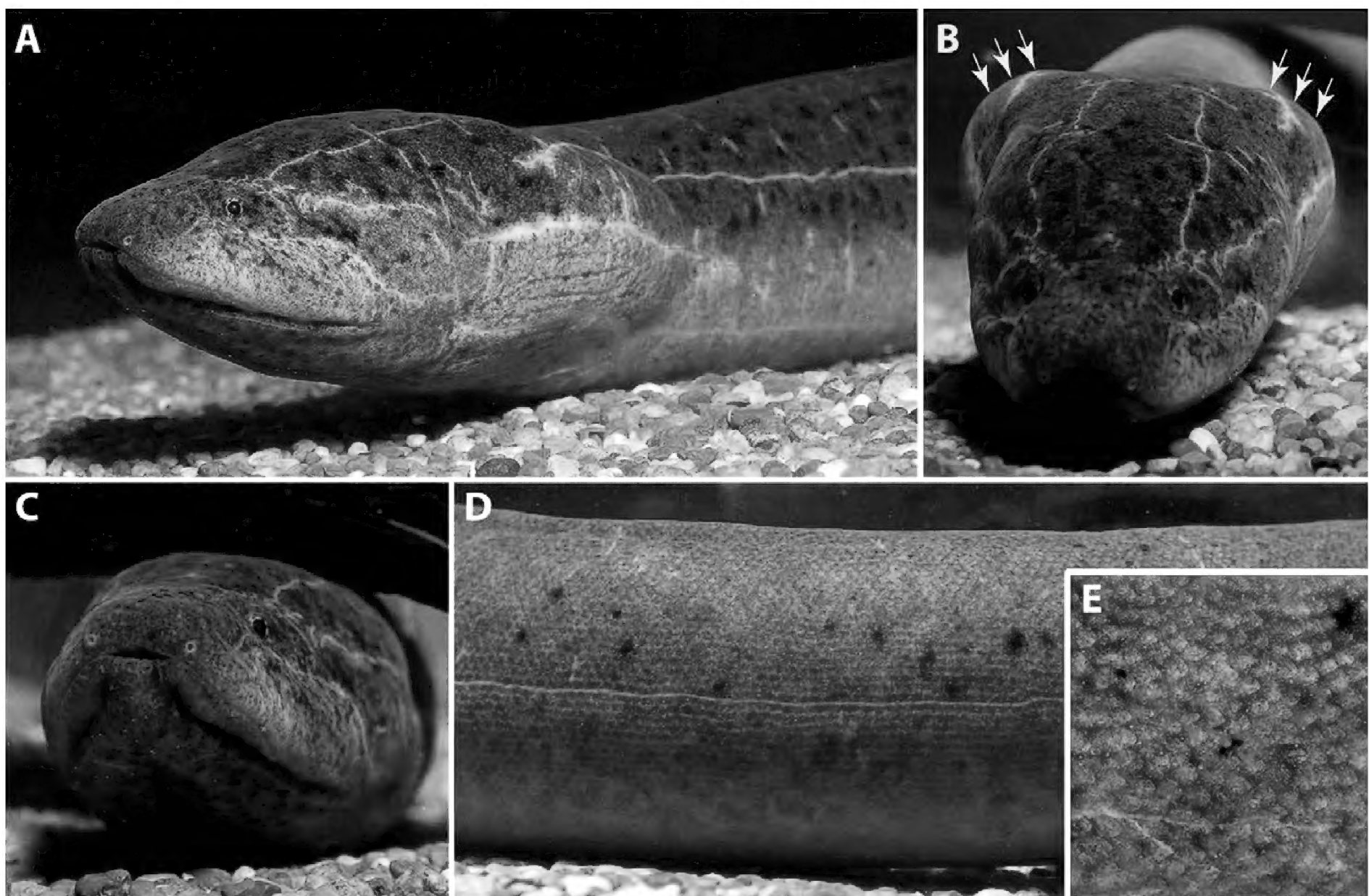


Figure 3. *Ophichthys cuchia*, TCWC 20288.01, not measured, ca. 600 mm TL, photographed in aquarium soon after collection. **A.** Head and anterior part of body, left side in lateral view. **B.** Head in anterodorsal view; arrows point to paired swellings on posterolateral part of head due to presence of air inside of suprabranchial chambers. **C.** Head in slight anterolateral view showing location of anterior nostrils. **D.** Left side of body, close to center, in lateral view, showing tiny cycloid scales and pale yellow lateral stripe along course of body lateral line. **E.** Close up of tiny cycloid scales on tail, left side in lateral view. Photographs by R. Britz (A, B) and K.W. Conway (C–E).

group, except for a group comprising three sequences from Assam, India. Sequences obtained from the four individuals of *O. cuchia* from Fort Bend Co., Texas, are dispersed throughout the *O. cuchia* lineage (Fig. 4B).

Discussion

In their review of Asian swamp eels in North America, Nico et al. (2019) reported the presence of live *Ophichthys cuchia* (as *Amphipnous cuchia*) in a single Houston food market visited in 2012. Soon after, Jordan et al. (2020) reported on the collection of *O. cuchia* (as *A. cuchia*) from a retention basin in urban Houston, based on a personal communication with one of us (A. Best). This previous report referred to multiple specimens of *O. cuchia* collected from retention ponds in Buffalo Run Park during surveys for game fishes by A. Best in 2019. Those specimens were not preserved but subsequent sampling events at the same locality in 2019, 2020, and 2021 produced an additional 26 specimens, all of which have been deposited in a museum collection and form the basis of this record. The majority of the collected specimens are over 600 mm TL (Fig. 5) and are likely adults. It is possible that these large individuals of *O. cuchia* were purchased in local markets and then released at this location, but like Jordan et al. (2020), we are convinced that this species is reproducing within Buffalo Run Park based on

the collection of multiple smaller specimens (Fig. 5): the smallest only 154 mm TL and likely young of the year. Based on information available from Banerji et al. (1981), *O. cuchia* can achieve a length of 60 mm in less than 30 days and at this size resemble adults in external appearance. It is unlikely that the smallest specimen that we collected at Buffalo Run Park was released there because only larger sized synbranchids (TL ≥ 550 mm) are typically traded in live fish markets in the USA (Nico et al. 2011, 2019). If correct, then the population of *O. cuchia* at Buffalo Run Park represents only the second established non-native population of this species in the USA.

Ophichthys cuchia is native to much of northern India, and adjacent countries (Talwar and Jhingran 1991; Nico et al. 2019) and is the target of both subsistence and commercial fisheries in at least Bangladesh and India. Based on import records examined by Nico et al. (2019), the majority of specimens of *O. cuchia* sold live in fish markets in the USA were originally exported from Bangladesh (Nico et al. 2019). Our investigation of COI sequences of *O. cuchia* suggests that the potential source of the invasive Texas population was likely specimens collected in the Ganges Delta region of Bangladesh and/or India. Though we lack precise locality data for most of the GenBank sequences that we analyzed (Appendix Table A1), we identified two mitochondrial haplotypes shared by individuals collected from Buffalo Run Park

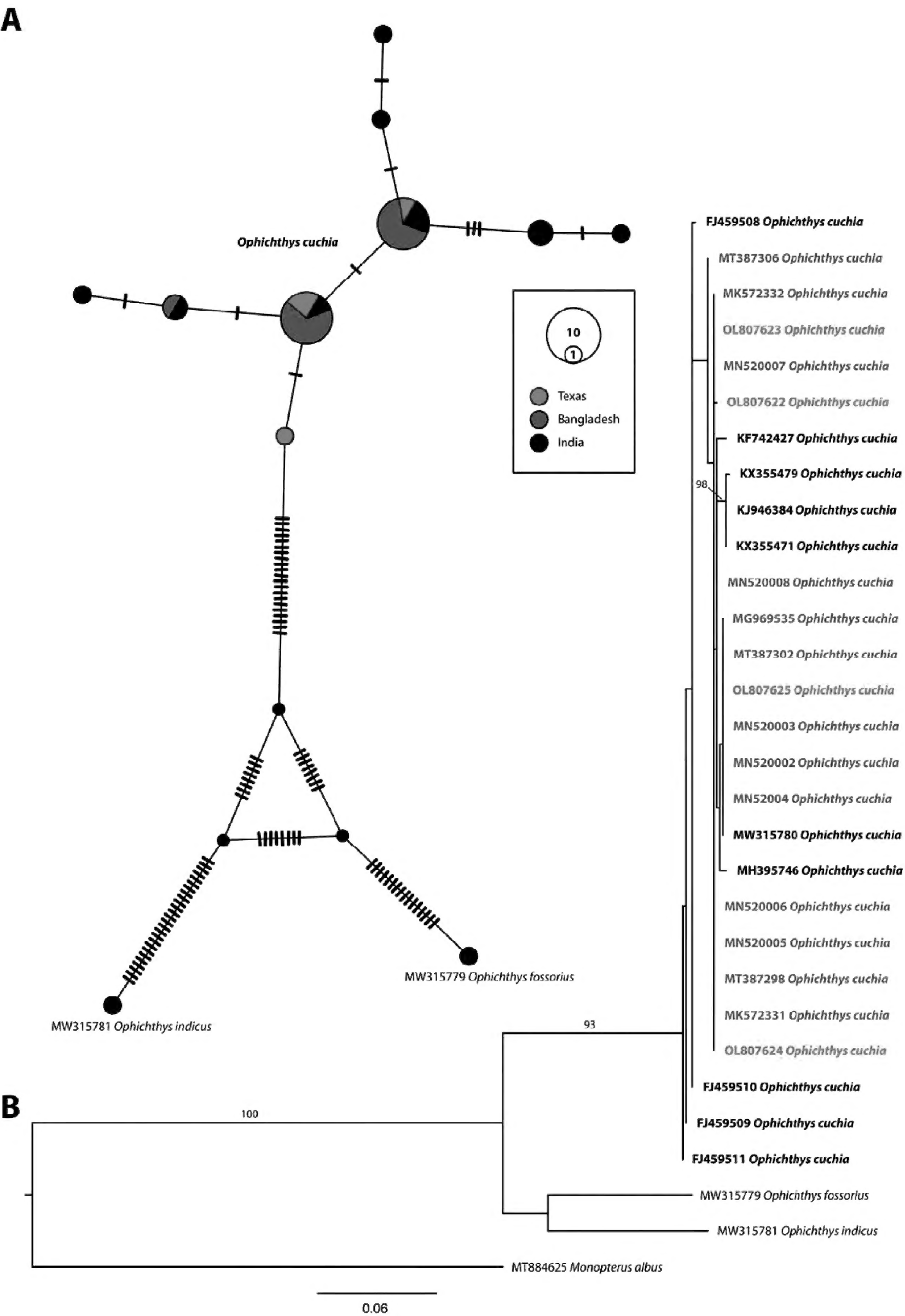


Figure 4. A. COI haplotype network for three species of *Ophichthys*. Circle size reflects haplotype frequency. Red, grey, and black fill indicates haplotypes detected in Texas, Bangladesh, and India, respectively. **B.** Maximum likelihood (ML) phylogram with the lowest log likelihood score (-lnL) obtained from analysis of COI dataset. Numbers above branches represent bootstrap values (>50%). Labels in red, grey, and black represent sequences from specimens collected in Texas, Bangladesh, and India, respectively.

and those also collected in eastern Bangladesh (Rahman et al. 2019) and West Bengal, India (Britz et al. 2021).

As already stated by Jordan et al. (2020), the presence of *O. cuchia* in waterbodies in the USA could represent a

serious threat to native species through the introduction of both novel predators and novel parasites. Though our sample size is low, our investigation of stomach contents of individuals of *O. cuchia* collected from Buffalo Run

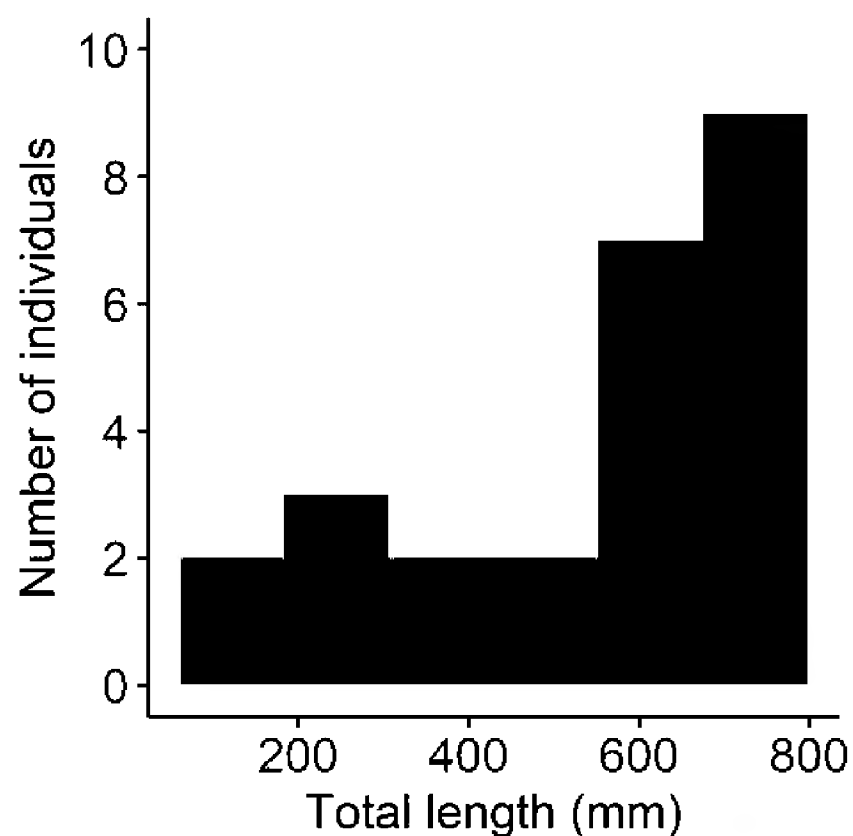


Figure 5. Histogram documenting the size (mm TL) of 25 individuals of *Ophichthys cuchia* collected from Buffalo Run Park, Fort Bend Co., Texas, USA between 2019 and 2021.

Park has confirmed that they are capable of consuming juvenile centrarchids, the adults of which are some of the most popular gamefish in Texas and support a billion-dollar recreational fishing industry. The close proximity between the retention ponds in Buffalo Run Park and drainage channels that connect with Sims Bayou is also troubling as flood events could easily facilitate the spread of *O. cuchia* to other water bodies within the Houston metro area. Worryingly, *O. cuchia* were collected from Buffalo Run Park before and after a severe winter storm event in February 2021, during which time air temperatures in the Houston metro area dropped to -10°C . This suggests that *O. cuchia* may be capable of surviving low temperatures for short periods, thermal refugia are present in Buffalo Run Park, or that specimens continue to be released at this location. Continued monitoring for *O. cuchia* at Buffalo Run Park and adjacent water bodies is recommended to assess the realized or potential ecological impact of the species. Long-term study of an introduced population of *Monopterus albus* in Florida, USA, suggests that this species may have minimal ecological effects based on a large proportion of empty stomachs and consumption of small fish as prey items (Hill and Watson 2007; Shafland et al. 2009). Regardless, the expanding non-native ranges of Asian swamp eels in the USA should continue to be monitored given the paucity of information on these species and the potential effect that they may have on invaded ecosystems (Taylor et al. 2018; Johnson et al. 2020).

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Authors' Contributions

Conceptualization: AB, JSP, KWC. Data curation: AKP, HB. Formal analysis: AB, AKP, HB, JSP, KWC. Visualization: JSP, KWC. Writing – original draft: AB, JSP, KWC.

References

- Bailey RM, Gans C (1998) Two new synbranchid fishes, *Monopterus roseni* from peninsular India and *M. desilvai* from Sri Lanka. Occasional Papers of the Museum of Zoology, The University of Michigan 726: 1–18.
- Bandelt H, Forster P, Röhl A (1999) Median-joining networks for inferring intraspecific phylogenies. *Molecular Biology and Evolution* 16: 37–48. <https://doi.org/10.1093/oxfordjournals.molbev.a026036>
- Banerji SR, Singh ML, Thakur NK (1981) Observations on natural breeding and larval development of the common mud-eel *Amphipnous cuchia* (Ham.). *Hydrobiologia* 79: 147–155. <https://doi.org/10.1007/bf00006122>
- Britz R (2019) Francis Hamilton's Gangetic Fishes in colour. A new edition of the 1822 monograph, with reproductions of unpublished coloured illustrations. Ray Society, London, UK, 453 pp.
- Britz R, Lalremsanga HT, Lalrotluanga, Lalramliana (2011) *Monopterus ichthyophoides*, a new species of scaled swamp eel (Teleostei: Synbranchiformes: Synbranchidae) from Mizoram, India. *Zootaxa* 2936: 51–58. <https://doi.org/10.11646/zootaxa.2936.1.2>
- Britz R, Sudasinghe H, Sykes D, Tharindu Ranasinghe RH (2020) *Ophichthys desilvai*, a poorly known synbranchid eel from Sri Lanka (Teleostei: Synbranchidae). *Ichthyological Exploration of Freshwaters* 30: 1–16. <https://doi.org/10.23788/IEF-1139>
- Britz R, Dahanukar N, Standing A, Philip S, Kumar B, Raghavan R (2021a) Osteology of '*Monopterus*' *roseni* with the description of *Rakthamichthys*, new genus, and comments on the generic assignment of the Amphipnous Group species (Teleostei: Synbranchiformes). *Ichthyological Exploration of Freshwaters* 30: 221–236. <https://doi.org/10.23788/ief-1163>
- Britz R, Standing A, Kumar B, Kripakaran M, Katwate U, Sundar RL, Raghavan R (2021b) *Ophichthys fossorius*, a poorly known South Indian swamp eel (Teleostei: Synbranchidae). *Ichthyological Exploration of Freshwaters* IEF-1173: 1–14. <https://doi.org/10.23788/ief-1173>
- Hamilton, F (1822) An account of the fishes found in the river Ganges and its branches. Archibald Constable and Company, Edinburgh, UK, 405 pp.
- Hill JE, Watson CA (2007) Diet of the nonindigenous asian swamp eel in tropical ornamental aquaculture ponds in west-central Florida. *North American Journal of Aquaculture* 69: 139–146. <https://doi.org/10.1577/A05-070.1>
- Johnson JR, Taylor AT, Long JM (2020) Estimating the invasion extent of Asian swamp eel (*Monopterus*: Synbranchidae) in an altered river of the south-eastern United States. *Marine and Freshwater Research* 72: 811–822. <https://doi.org/10.1071/mf20257>
- Jordan F, Nico LG, Huggins KA, Martinat PJ, Martinez DA, Rodrigues VL (2020) Discovery of a reproducing wild popula-

tion of the swamp eel *Amphipnous cuchia* (Hamilton, 1822) in North America. *BioInvasions Records* 9: 367–374. <https://doi.org/10.3391/bir.2020.9.2.22>

Kumar S, Stecher G, Li M, Knyaz C, Tamura K (2018) MEGA X: Molecular Evolutionary Genetics Analysis across computing platforms. *Molecular Biology and Evolution* 35: 1547–1549. <https://doi.org/10.1093/molbev/msy096>

Leigh JW, Bryant D (2015) PopART: full-feature software for haplotype network construction. *Methods in Ecology and Evolution* 6: 1110–1116. <https://doi.org/10.1111/2041-210x.12410>

Liem KF (1968) Geographical and taxonomic variation in the pattern of natural sex reversal in the teleost fish order Synbranchiformes. *Journal of Zoology, London* 156: 225–238. <https://doi.org/10.1111/j.1469-7998.1968.tb05930.x>

Müller J (1840) Ueber Nebenkiemen und Wundernetze. *Archiv für Anatomie, Physiologie und Wissenschaftliche Medicin* 7: 101–142.

Nico LG, Sharp P, Collins TM (2011) Imported Asian swamp eels (Synbranchidae: *Monopterus*) in North American live food markets: Potential vectors of non-native parasites. *Aquatic Invasions* 6: 69–76. <https://doi.org/10.3391/ai.2011.1.08>

Nico LG, Ropicki AJ, Kilian JV, Harper M (2019) Asian swamp eels in North America linked to the live-food trade and prayer-release rituals. *Aquatic Invasions* 14: 775–814. <https://doi.org/10.3391/ai.2019.14.4.14>

Rahman MM, Noren M, Mollah AR, Kullander SO (2019) Building a DNA barcode library for the freshwater fishes of Bangladesh. *Scientific Reports* 9: 1–10. <https://doi.org/10.1038/s41598-019-45379-6>

Rosen DE, Greenwood PH (1976) A fourth Neotropical species of synbranchid eel and the phylogeny and systematics of synbranchiform fishes. *Bulletin of the American Museum of Natural History* 157: 1–69.

Shafland PL, Gestring KB, Stanford MS (2009) An assessment of the Asian swamp eel (*Monopterus albus*) in Florida. *Reviews in Fisheries Science* 18: 25–39. <https://doi.org/10.1080/10641260903225542>

Swainson W (1839) On the natural history and classification of fishes, amphibians, & reptiles, or monocardian animals. Volume 2. Spottiswoode, London, UK, 452 pp. <https://doi.org/10.5962/bhl.title.62140>

Talwar PK, Jhingran AG (1991) Inland fishes of India and adjacent countries. Volume 2. Oxford & IBH Publishing Co., New Delhi, Bombay, Calcutta, India, 615 pp.

Taylor AT, von Schmeling H, Long JM (2018) Photographs of wading bird depredation update invasion extent of *Monopterus albus* (Asian Swamp Eel). *Southeastern Naturalist* 17: N72–76. <https://doi.org/10.1656/058.017.0408>

Ward RD, Zemlak TS, Innes BH, Last PR, Hebert PD (2005) DNA barcoding Australia’s fish species. *Philosophical Transactions of the Royal Society B: Biological Sciences* 360: 1847–1857. <https://doi.org/10.1098/rstb.2005.1716>

Zwickl DJ (2006) Genetic algorithm approaches for the phylogenetic analysis of large biological sequence datasets under the maximum likelihood criterion. PhD Dissertation, University of Texas, Austin, USA, 115 pp.

Appendix

Table A1. GenBank numbers for COI sequences used in this study.

Species	GenBank no.	Locality/source
<i>Ophichthys cuchia</i>	OL807622	Fort Bend Co., Texas, USA/this study
<i>Ophichthys cuchia</i>	OL807623	Fort Bend Co., Texas, USA/this study
<i>Ophichthys cuchia</i>	OL807624	Fort Bend Co., Texas, USA/this study
<i>Ophichthys cuchia</i>	OL807625	Fort Bend Co., Texas, USA/this study
<i>Ophichthys cuchia</i>	MK572331	Chittagong Division, Bangladesh/Rahman et al. 2019
<i>Ophichthys cuchia</i>	MK572332	Sylhet Division, Bangladesh/Rahmannn et al. 2019
<i>Ophichthys cuchia</i>	MT387298	Tangail, Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MT387306	Bagerhat, Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MT387302	Bogra, Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MG969535	Chalan Beel, Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520006	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520005	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520008	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520007	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520004	Bangladesh/GenBank, unpublished

Species	GenBank no.	Locality/source
<i>Ophichthys cuchia</i>	MN520003	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MN520002	Bangladesh/GenBank, unpublished
<i>Ophichthys cuchia</i>	MW315780	West Bengal, India/Britz et al. 2021
<i>Ophichthys cuchia</i>	KX355479	Assam, India/GenBank, unpublished
<i>Ophichthys cuchia</i>	KX355471	Assam, India/GenBank, unpublished
<i>Ophichthys cuchia</i>	KJ946384	Assam, India/GenBank, unpublished
<i>Ophichthys cuchia</i>	KF742427	India/GenBank, unpublished
<i>Ophichthys cuchia</i>	FJ459509	India/GenBank, unpublished
<i>Ophichthys cuchia</i>	FJ459511	India/GenBank, unpublished
<i>Ophichthys cuchia</i>	FJ459510	India/GenBank, unpublished
<i>Ophichthys cuchia</i>	FJ459508	India/GenBank, unpublished
<i>Ophichthys cuchia</i>	MH395746	India/GenBank, unpublished
<i>Ophichthys fossorius</i>	MW315779	Kerala, India/Britz et al. 2021
<i>Ophichthys indicus</i>	MW315781	Maharashtra, India/Britz et al. 2021
<i>Monopterus albus</i>	MT884625	Guangdong, China/GenBank, unpublished